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Hypoxia's impact on pelagic fish populations in Lake Erie: a tale of two planktivores

Joshua P. Stone, Kevin L. Pangle, Steven A. Pothoven, Henry A. Vanderploeg, Stephen B. Brandt, Tomas O. Höök, Thomas H. Johengen, and Stuart A. Ludsin

Abstract: Whether bottom hypoxia has long-lasting consequences for pelagic fish populations remains speculative for most ecosystems. We explored hypoxia's influence on two pelagic zooplanktivores in Lake Erie that have different thermal preferences: cold-water rainbow smelt (*Osmerus mordax*) and warm-water emerald shiners (*Notropis atherinoides*). To assess acute effects, we combined predictive bioenergetics-based modeling with field collections made across the hypoxic season in central Lake Erie during 2005 and 2007. To assess chronic effects, we related fishery-independent and fishery-dependent catches with hypoxia severity and top predator (walleye, *Sander vitreus*) abundance during 1986–2014. As our modeling predicted, hypoxia altered rainbow smelt movement and distributions, leading to avoidance of cold, hypoxic bottom waters. In response, diets shifted from benthic to pelagic organisms, and consumption and energetic condition declined. These changes were lacking in emerald shiners. Our long-term analyses showed rainbow smelt abundance and hypoxia to be negatively related and suggested that hypoxia avoidance increases susceptibility to commercial fishing and walleye predation. Collectively, our findings indicate that hypoxia can negatively affect pelagic fish populations over the long term, especially those requiring cold water.

Résumé : Les éventuelles conséquences durables de l'hypoxie de fond sur les populations de poissons pélagiques relèvent toujours du domaine de la conjecture pour la plupart des écosystèmes. Nous avons exploré l'influence de l'hypoxie sur deux poissons zooplanctonivores pélagiques dans le lac Érié présentant différentes préférences thermiques, soit l'éperlan arc-en-ciel (*Osmerus mordax*), d'eau froide, et le mené vert (*Notropis atherinoides*), d'eau plus chaude. Pour évaluer les effets aigus, nous avons combiné la modélisation prédictive basée sur la bioénergétique à des prélèvements sur le terrain réalisés dans la partie centrale du lac Érié durant la période hypoxique en 2005 et 2007. Pour évaluer les effets chroniques, nous avons relié les prises indépendantes de la pêche et les prises dépendantes de la pêche à l'intensité de l'hypoxie et à l'abondance de prédateurs sommitaux (doré jaune, *Sander vitreus*) de 1986 à 2014. Comme le prédit notre modélisation, l'hypoxie modifie les déplacements et la répartition des éperlans arc-en-ciel, menant à leur évitement des eaux de fond hypoxiques froides. En réaction, les régimes alimentaires passent d'organismes benthiques à des organismes pélagiques, et la consommation et la condition énergétique diminuent. Ces changements ne sont pas observés chez les menés verts. Nos analyses sur le long terme montrent une relation négative entre l'abondance des éperlans arc-en-ciel et l'hypoxie et donnent à penser que l'évitement de l'hypoxie accroît la vulnérabilité à la pêche commerciale et à la prédation par les dorés jaunes. Collectivement, nos constatations indiquent que l'hypoxie peut avoir un effet négatif sur les populations de poissons pélagiques sur le long terme, particulièrement celles de poissons qui ont besoin d'eau froide. [Traduit par la Rédaction]

Introduction

Human-driven environmental change is threatening the world's aquatic ecosystems and the services that they provide to society (Vitousek et al. 1997; Foley et al. 2005; Scheffers et al. 2016). One such stressor that has become a growing problem worldwide is reduced dissolved oxygen availability (i.e., hypoxia), owing to the combined effects of cultural eutrophication and climate warming (Kennish 2002; Diaz and Rosenberg 2008; Breitburg et al. 2018). Hypoxia is of particular concern to management agencies because of its potential to reduce fisheries production through direct mortality, as well as through indirect (sublethal) effects on habitat availability and use, which could negatively influence foraging, growth, and eventual survival to the fishery (Eby et al. 2005; Breitburg et al. 2009b; Ludsin et al. 2009). In addition, hypoxia avoidance can cause fish to aggregate (e.g., Vanderploeg et al. 2009b; Zhang et al. 2009; Craig 2012), which could hamper effective fisheries management by altering catchabilities both in the fishery (Langseth et al. 2014; Switzer et al. 2015; Purcell et al. 2017)

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Fig. 1. Time series of dissolved oxygen (DO) and fish abundance in central Lake Erie, 1987–2014. Data include (A) the percentage of interpolated coverage area during August with bottom DO < 4 mg·L^{-1} (interpolated area spans the monitoring area in the USEPA's Great Lakes Environmental database: http://www.exchangenetwork.net/data-exchange/glenda/) and the estimated population size of age 2+ walleye in Lake Erie (data from Lake Erie Walleye Task Group; Wills et al. 2018); and (B) average catch per unit effort (CPUE; number of individuals per trawl minute) of adult (age 2+) rainbow smelt and emerald shiner caught in fishery-independent trawl surveys conducted by the Ohio Department of Natural Resources – Division of Wildlife in Lake Erie's central basin during fall (late September through mid-October).
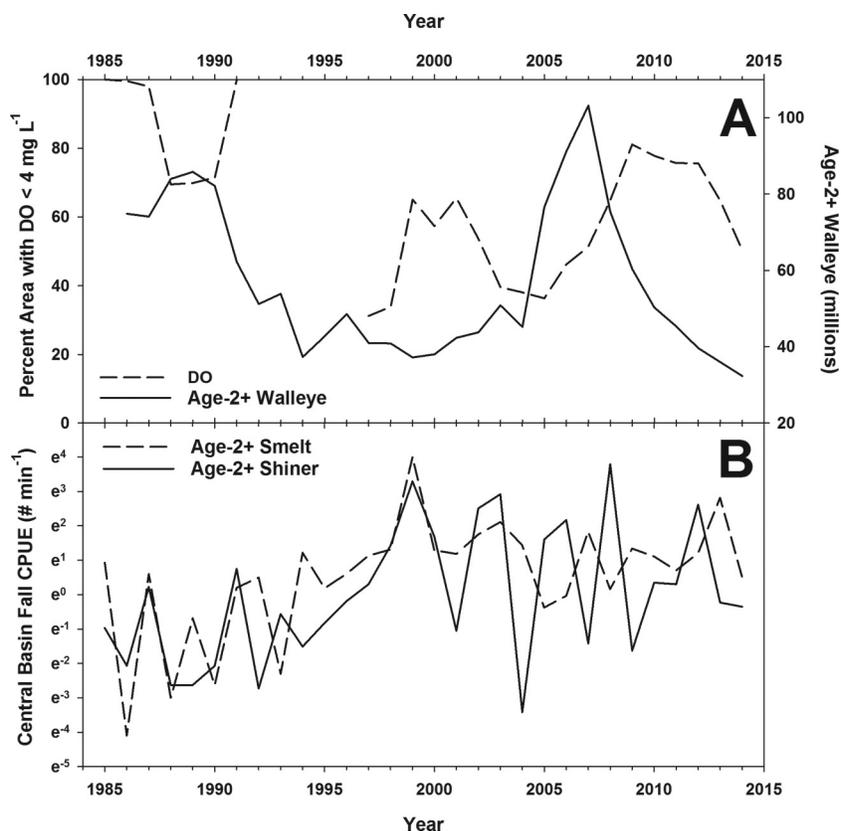
and in fishery-independent surveys of abundance (Kraus et al. 2015a; Langseth et al. 2016; Froehlich et al. 2017).

Despite the potential for hypoxia to negatively affect fish populations, and the dynamics of the fisheries that they support, evidence that hypoxia has long-term effects on fish population and fishery production potential remains scarce (Breitburg et al. 2009a, 2009b, 2015; Rose et al. 2009). The reasons for our inability to detect relationships between hypoxia and long-term fish population and fishery dynamics are numerous. They include, but are not limited to (i) a lack of mechanistic knowledge regarding the impacts of hypoxia on aquatic food webs and the fished population at the correct spatiotemporal scales (e.g., long-term studies over large spatial scales); (ii) a lack of long-term monitoring data on key indicator variables; (iii) compensatory mechanisms that offset the impacts of hypoxia during other times of the year; (iv) spatiotemporal variability in habitat conditions, fish behavior, and fishing; and (v) confounding effects of other potentially more dominant ecological phenomena or environmental stressors (Breitburg et al. 2009a, 2015; Rose et al. 2009). Knowledge of whether hypoxia has population-level effects on pelagic fishes — which typically do not use bottom waters (where hypoxia typically occurs) — has remained especially elusive (Ludsin et al. 2009; Zhang et al. 2009; Ekau et al. 2010; see Roman et al. 2019 for a review on this topic). This gap in knowledge is partially due to these species only becoming the focus of investigation during the past decade in eutrophic systems such as Chesapeake Bay (e.g., Ludsin et al. 2009; Adamack et al. 2012), the northern Gulf of Mexico (e.g., Hazen et al. 2009; Zhang et al. 2009, 2014), Lake Erie (e.g., Roberts et al. 2009; Vanderploeg et al. 2009b; Pothoven et al.

2012), Puget Sound, Washington (Parker-Stetter et al. 2009; Sato et al. 2016), and the California Current System (Chan et al. 2008). Thus, the need exists to better understand whether the short-term (acute), local effects of hypoxia on pelagic and benthopelagic fish movement behavior, habitat use, and foraging, which have predominantly been the focus of these investigations, have longer-term, population-level consequences.

One ecosystem for which the long-term effect of hypoxia on pelagic and benthopelagic fishes remains unresolved is Lake Erie. The extent of seasonal bottom hypoxia has varied widely in its largest (central) basin during the past century, with it noticeably increasing during the past decade (Fig. 1A; Rosa and Burns 1987; Hawley et al. 2006; Zhou et al. 2013), owing to human-driven eutrophication and possible contributions from climate change (Scavia et al. 2014; Rucinski et al. 2016; Watson et al. 2016). During this same period, the abundances of rainbow smelt (*Osmerus mordax*; Osmeridae), a cold-water, benthopelagic species, and emerald shiner (*Notropis atherinoides*; Cyprinidae), a warm-water, epipelagic species, have substantially varied (Fig. 1B) for reasons that remain unclear. Because these two species typically occupy different areas of the water column in central Lake Erie, in large part owing to their thermal growth optima (see section on Study species below), the study of their dynamics provides a way to explore if and how hypoxia can differentially affect pelagic fish populations.

Learning whether hypoxia has been affecting these species is important to Lake Erie management agencies for several reasons. First, both species are preferred prey of walleye (*Sander vitreus*; Knight et al. 1984; Knight and Vondracek 1993; ODNR–DOW 2018),

which supports recreational and commercial fisheries in Lake Erie that are valuable to the region's economy (Hatch et al. 1987; Vandergoot et al. 2010; ODNR–DOW 2018). Second, rainbow smelt and emerald shiners consume zooplankton and hence may influence other zooplanktivorous fishes, such as gizzard shad (*Dorosoma cepedianum*), alewife (*Alosa pseudoharengus*), white perch (*Morone americana*), and yellow perch (*Perca flavescens*), through competitive and (or) predator interactions (Hartman et al. 1992; Pothoven et al. 2009, 2012). Finally, rainbow smelt has historically supported a large commercial fishery in Lake Erie (Henderson and Nepszy 1989; OMNRF 2016), with the emerald shiner also being important to the lake's baitfish industry (Nielsen 1982; Knight and Vondracek 1993; Meronek et al. 1997).

At present, a long-term assessment of the effects of hypoxia on rainbow smelt and emerald shiner has not yet been conducted in any ecosystem. Short-term investigations into habitat quality, habitat use, and foraging have suggested, however, the potential for hypoxia to influence the dynamics of these species in central Lake Erie. First, in a study that modeled habitat quality of these species in central Lake Erie during 1987–2005 (Arend et al. 2011), bottom hypoxia was shown to reduce the amount of habitat that can support positive growth for both adult rainbow smelt (by ~35%) and adult emerald shiners (by ~12%). In the case of rainbow smelt, lost access to cold thermal habitat along the lake bottom was the primary driver of this reduction, whereas lost access to prey was the driver of the emerald shiner decline (Arend et al. 2011). Second, consumption (measured as daily ration) by rainbow smelt and emerald shiner declined during the hypoxic period, although the role of hypoxia in this decline was somewhat questionable for emerald shiner (Pothoven et al. 2009, 2012). The decline in consumption by rainbow smelt was attributed to several mechanisms: (*i*) hypolimnetic (bottom) hypoxia limiting access to benthic macroinvertebrate prey (Pothoven et al. 2009); (*ii*) zooplankton using the hypoxic hypolimnion and warm (suboptimal) epilimnion as a refuge from planktivory by rainbow smelt (Vanderploeg et al. 2009a, 2009b; Pothoven et al. 2012); and (*iii*) competition for zooplankton occurring in the thin layer of the metalimnion (just above the hypoxic zone), which contains suitably cold thermal habitat for growth (Pothoven et al. 2012). Third, reduced access to bottom waters has been hypothesized to increase the vulnerability of prey fishes such as rainbow smelt and emerald shiners to piscivorous walleye (Brandt et al. 2011), as well as simultaneously increase access to commercial fishers that might fish the edges of the hypoxic layer (sensu Kraus et al. 2015a; Purcell et al. 2017).

While these studies have collectively shown the capacity of hypoxia to negatively influence habitat quality and use for rainbow smelt and emerald shiners in the short term, questions remain that we view as essential to help understand whether linkages truly exist between bottom hypoxia and the long-term dynamics of these two species. First, do hypoxia-driven reductions in habitat quality and altered foraging distributions have consequences for rainbow smelt and emerald shiner performance (e.g., growth, energetic health)? For rainbow smelt, we predicted that bottom hypoxia would reduce foraging on benthic macroinvertebrate prey, as well as access to cold-water habitat associated with the hypoxic bottom layer, both of which would lead to reduced somatic growth and energetic condition. For emerald shiners, we also predicted hypoxia would negatively affect foraging, growth, and energetic condition, but through a different mechanism. Analogous to what Ludsin et al. (2009) found for Chesapeake Bay anchovy (*Anchoa mitchilli*; Engraulidae), which also is a zooplanktivorous, epipelagic, warm-water species, we expected that hypoxia would limit emerald shiner performance by reducing access to zooplankton. In other words, zooplankton would use the bottom hypoxic layer as a refuge from predation. Second, do long-term, population-level trends in rainbow smelt and emerald shiner track the severity of hypoxia? While we did not expect to find meaningful relation-

ships between hypoxia and the long-term demographics of these species, owing to the many other factors that can affect prey-fish demographics (sensu Breitburg et al. 2009a, 2009b; Rose et al. 2009), the recent availability of long-term dissolved oxygen data from the US Environmental Protection Agency (USEPA) and the literature (Zhou et al. 2015) allowed us to ask this question.

To answer these questions, we combined habitat quality (growth rate potential, GRP, which is akin to the "fundamental niche"; Brandt et al. 1992) modeling with site-specific field collections and analyses of long-term datasets. First, we present results from a spatially explicit, bioenergetics-based GRP model, which quantified habitat quality for rainbow smelt and emerald shiners throughout the water column over large spatial scales before, during, and (or) after the hypoxic season in 2005 and 2007. Second, we present site-specific field observations of fish spatial distributions (both horizontal and vertical), diets, body size, and energetic condition (health) before, during, and after hypoxia in 2005. Third, we relate long-term (1986–2014) catch-per-unit-effort (CPUE) data for rainbow smelt (fishery-independent and fishery-dependent) and emerald shiner (fishery-independent) to annual indices of hypoxia severity and walleye predators. In addition to discussing our findings and identifying needed research, we discuss the implications for fishery management in Lake Erie and other freshwater and marine ecosystems that are experiencing bottom hypoxia.

Methods

Study system

Lake Erie, which is the 11th largest lake in the world (by area), has a long history of hypolimnetic (bottom) hypoxia (Rosa and Burns 1987). In fact, bottom hypoxia is considered a natural phenomenon in its voluminous central basin (Delorme 1982). Because central Lake Erie is deep enough to stratify (mean depth = 18.3 m), but shallow enough that the thermocline can set up relatively close to the lake bottom (typically <6 m from the bottom; Rosa and Burns 1987), the volume of hypolimnetic water that is cut off from surface aeration is small. In turn, dissolved oxygen (DO) can be depleted before fall turnover, thus leading to bottom hypoxia (<4 mg $O_2 \cdot L^{-1}$) during late summer through early fall (Charlton 1980; Rosa and Burns 1987). Even so, the rate of DO depletion, as well as the extent of hypoxia, can be modified by human activities (Rosa and Burns 1987; Bertram 1993; Rucinski et al. 2016). For example, excessive nutrient inputs led to large hypoxic areas during the 1950s–1970s (Beeton 1963), and phosphorus abatement programs (Dolan 1993) during the late 1980s through the mid-1990s reduced central-basin hypoxia (Bertram 1993; Makarewicz and Bertram 1991; Charlton et al. 1993). More recently, the extent and duration of bottom hypoxia has increased to levels on par with those during the height of cultural eutrophication in the 1950s–1970s (Burns et al. 2005; Zhou et al. 2013; Scavia et al. 2014). The exact causal mechanisms for this recent increase in hypoxia are not fully understood, however, although it does coincide with increased nutrient inputs from non-point sources and climate warming (Rucinski et al. 2010; Scavia et al. 2014; Watson et al. 2016).

Study species

Rainbow smelt is a nonindigenous planktivore that invaded Lake Erie during the 1930s (Scott and Crossman 1973). It has become a naturalized component of Lake Erie's fish community. At one point, rainbow smelt supported Lake Erie's largest commercial fishery; however, average commercial landings of this species have declined 20%–40% relative to each previous decade since the 1980s, with average landings since 2010 only being ~25% of the 1980s' average (http://www.glfc.org/great-lakes-databases.php). Even so, rainbow smelt is still considered an important prey item for native cool- and cold-water piscivores in Lake Erie, including wall-

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Table 1. Description of the data used in this study, which was collected during August, September, and October 2005 and September 2007 in central Lake Erie.

Sampling gear and lab analyses	Variables measured	2005			2007	
		CTD sites	Diel transects	Long transects	CTD sites	Long transects
Vertical CTD casts	Dissolved oxygen, temperature	+	—	—	+	—
Plankton sampling system and zooplankton nets	Temperature	—	+	+	—	+
	Dissolved oxygen	—	+	+	—	+
	Zooplankton biomass	—	+	+	—	—
Fish acoustics	Fish biomass	—	+	+	—	+
Fish trawls	Fish abundance and composition	+	+	—	+	—
Laboratory analysis	Fish total length, wet and dry mass, diet composition, diet biomass, and energy density	—	+	—	—	—

Note: Collections were made at specific stations (conductivity–temperature–depth (CTD) sites), along "short" (5 km) transects every 4 h over 24 h (diel transects) and across "long" (15–60 km) transects sampled once each during the day and night (long transects). A "+" indicates that sampling of that type occurred during that time period, whereas a "—" indicates that sampling did not occur.

eye, burbot (*Lota lota*), and both native (e.g., lake trout, *Salvelinus namaycush*) and non-native salmonines (Ryan et al. 1999; Stapanian et al. 2011; Madenjian et al. 2018). While Lake Erie rainbow smelt is considered a pelagic planktivore (Bidgood 1961), its diet can be broad at times, consisting of cladoceran zooplankton, benthic macroinvertebrates, and small (larval) fish (Dermott et al. 1999; Pothoven et al. 2009, 2012). As in their native range (Parker-Stetter et al. 2006), rainbow smelt in Lake Erie typically reside in the hypolimnion or lower metalimnion during stratified periods (Dermott et al. 1999; Ryan et al. 1999; Rudstam et al. 2003). Its use of bottom waters during the summer is especially important because adult growth is best at cold temperatures (10–12 °C), with temperatures above 20 °C considered lethal (Lantry and Stewart 1993).

The emerald shiner, a pelagic species native to Lake Erie, is a dominant component of central Lake Erie's fish community and an important prey for abundant top predators such as walleye (Knight et al. 1984; Knight and Vondracek 1993; Madenjian et al. 2018). Although emerald shiners will consume benthic macroinvertebrates when available in the water column (e.g., emerging Chironomidae pupae; Pothoven et al. 2009), this species typically consumes cladoceran zooplankton and thus is considered a planktivore (Ewers 1933; Muth and Busch 1989; Hartman et al. 1992). Emerald shiners reside primarily in the epilimnion, schooling in it (especially at the surface) by day and dispersing throughout it at night (Trautman 1981; Schaeffer et al. 2008). The emerald shiner has an optimum temperature for growth near 25 °C (McCormick and Kleiner 2002) and is considered a warm-water species. While the emerald shiner is not recreationally fished, it does support an important baitfish industry in Lake Erie (Nielsen 1982; Knight and Vondracek 1993; Meronek et al. 1997).

For both study species, the physiological limit of hypoxia tolerance has not been experimentally tested. However, both species have been shown to avoid hypoxic waters in Lake Erie (Vanderploeg et al. 2009), with rainbow smelt being more sensitive to low DO than emerald shiners (Arend et al. 2011).

General overview of field measurements and collections

Field data and sample collections to support modeling and laboratory analyses were conducted during 2005 and 2007 as part of the International Field Years on Lake Erie (IFYLE) Program (Hawley et al. 2006; https://www.glerl.noaa.gov/res/projects/ifyle/). Below, we provide a general overview of our activities before providing detailed methods afterwards.

During 2005, we mapped the areal extent of the hypoxic zone, measured fish vertical and horizontal distributions in relation to habitat quality (i.e., DO, temperature, and zooplankton), and collected fish for diet, growth, and energetic condition analyses (Table 1). To measure the size of the hypoxic zone, we conducted vertical casts with a DO sensor (Model 13, Sea-Bird Electronics,

Bellevue, Washington) that was attached to a Sea-Bird 911+ conductivity–temperature–depth (CTD) profiler at fixed sites (Fig. 2, top panel) on a monthly basis during July through early October, which spanned the hypoxia season. To quantify habitat quality and fish habitat use before, during, and after the peak hypoxic period, we combined continuous data collections using towed instruments with site-specific CTD profiling and net collections (Table 1). To obtain continuous data, we used a plankton sampling system (PSS) and fish hydroacoustics to sample physico-chemical and biological attributes throughout the water column across both long (~15 to ~60 km) transects and short (5 km) "diel" transects (Fig. 2, top panel). Each long transect was sampled when sunlight was present (hereinafter, "daytime"; at least 1 h before sunset, including morning and afternoon hours) and when absent (hereinafter, "nighttime"; at least 1 h after sunset, including late evening and early morning hours). By contrast, we sampled each short (diel) transect every 4 h over a 24-h period. Neither the daytime or nighttime periods of the long transects included the crepuscular period (i.e., dusk or dawn), to avoid confounding effects of rapid changes in the light environment. For the same reason, each crepuscular period was sampled within its own 4-h time block for the short diel sampling. To obtain site-specific data and biological samples, we conducted vertical CTD casts and zooplankton net tows, as well as fish trawling (both bottom and midwater), at the start, middle, and end of each long continuous transect, during both day and night (Table 1). Similar site-specific sampling with the CTD and nets was made every 4 h over a 24-h period on alternating ends of each short diel station, which typically occurred the week after the long-transect sampling.

Owing to poor weather during 2005, only one long transect (transect B) and one short (diel) transect (station B, located in the midpoint of transect B) were consistently sampled before (10–11 and 15–16 August, respectively), during (7–8 and 17–18 September, respectively), and immediately after (12–13 and 13–14 October, respectively; beginning ~6 days after water column destratification) the hypoxic season (Fig. 2). Hence, we only present habitat quality, habitat use, diet, fish size, and energetic condition from those two transects herein.

During 2007, we towed the PSS and fish hydroacoustic gear throughout the central basin during the peak hypoxia period (4–11 September) to both estimate the size of the hypoxic zone and to explore the use of the hypoxic edges by fish. This sampling was designed to test two hypotheses. First, we wanted to learn whether hypoxia caused fish to aggregate at the edges of the hypoxic zone, which had been reported for benthic species in the northern Gulf of Mexico (Craig and Crowder 2005). Second, we wanted to explore whether hypoxia could cause a thermal–oxygen "squeeze" (sensu Coutant 1985) that could potentially limit movement of rainbow smelt between the hypoxic central basin and

Fig. 2. Map of Lake Erie sampling sites during 2005 (top panel) and 2007 (bottom panel). "Long" survey transects (black lines), "short" diel transects (horizontal white bars), and sites of vertical conductivity–temperature–depth (CTD) casts (white circles) were carried out in the central basin of Lake Erie during the summer growing season. The letters B (2005) and D (2007) refer to specific transects highlighted in the Results. This figure was created using ArcGIS software by Esri, and bathymetry data were acquired from National Geophysical Data Center (1999).
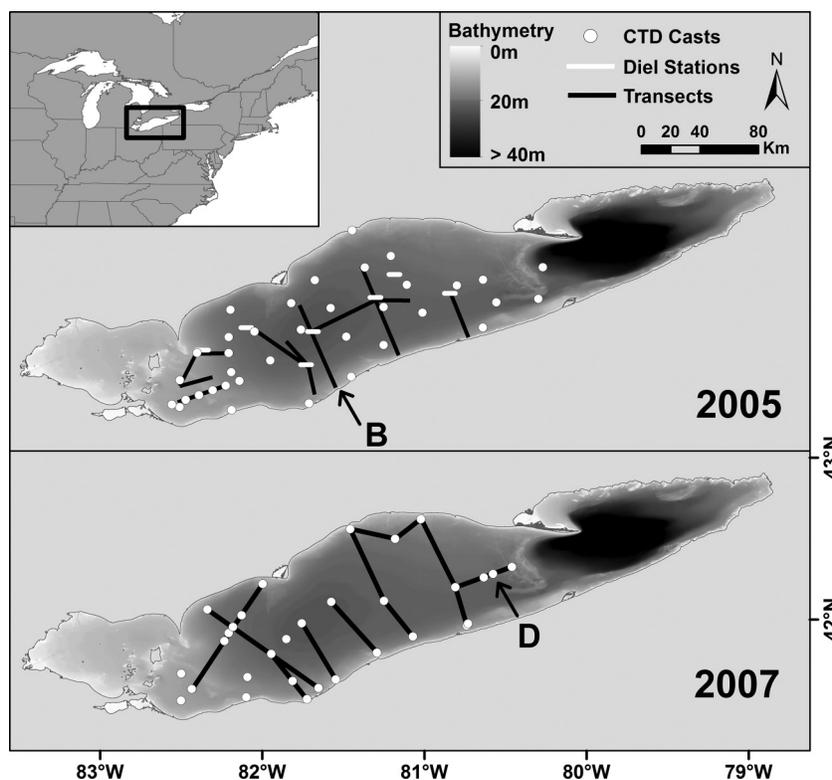
oxygenated east basin. For this latter question, we focused on an approximately 30-km transect located near the interface of the central and eastern basin (transect D; Fig. 2, bottom panel), which became shallow (~16 m depth) owing to the Clear Creek and Pennsylvania ridge. Fish midwater and bottom trawls, supplemented by CTD casts, also were periodically collected to help better define the hypoxic zone and determine the composition of fish being insonified by the hydroacoustics gear.

Plankton sampling system (PSS) collections

Along the long and short (diel) transects sampled during 2005, we quantified physicochemical attributes and the lower food web using a PSS, the details of which can be found in Vanderploeg et al. (2009a, 2009b). In brief, the PSS consisted of a CTD, a mini optical plankton counter (OPC), and a DO sensor mounted on a V-fin. The PSS was towed at ~2.5 m·s⁻¹ along a sinusoidal path from 1–2 m off the bottom to ~2 m from the surface. Georeferenced data collected by the sensors were averaged over 0.5-s intervals and logged by an onboard computer. The PSS measured depth distribution of temperature, DO, and the number and biomass of zooplankton-sized particles. These particles were converted into zooplankton wet mass following established methods that have shown that the PSS can accurately estimate observed zooplankton sizes, counts, and biomass in Great Lakes ecosystems with low suspended particulate matter, such as central Lake Erie during the summer hypoxic period (Liebig et al. 2006; Vanderploeg et al. 2009a). If any bias occurred, it would be an overestimate of zooplankton biomass, owing to suspended particulates being misidentified as zooplankton (Liebig et al. 2006). During the 2007 cruise, the OPC was

nonfunctional, and only DO and temperature were recorded from the PSS.

Habitat quality and use

To generate predictions on the relative effect of hypoxia on rainbow smelt and emerald shiner habitat quality, we calculated the growth rate potential (GRP; g·g⁻¹·day⁻¹) for adult (age 1+) emerald shiners, as well as for yearling (age 1) and adult (age 2+) rainbow smelt, before (August), during (September), and immediately after (October) hypoxia along transect B in 2005 and along transect D in 2007. We only present results from the yearling rainbow smelt GRP modeling herein because they offer a more conservative prediction of the influence of bottom hypoxia and temperature on GRP than do the results from the adult rainbow smelt modeling (see online Supplemental Information[1]).

GRP has been successfully used to describe habitat quality at fine spatial scales for both freshwater and marine fishes (e.g., Brandt et al. 1992; Kraus et al. 2015b), including those found in Lake Erie (Arend et al. 2011; Brandt et al. 2011). Our calculations were made using a spatially explicit bioenergetics model along with actual observations of temperature and DO collected by the PSS during daylight transects (see previous section), as both rainbow smelt and emerald shiners primarily rely on vision to find prey. We used models that were specifically developed to evaluate the effects of hypoxia on rainbow smelt and emerald shiners in Lake Erie (Arend et al. 2011; see Appendix A for details on model structure and parameterization). We also conducted sensitivity analyses where we removed the effect of DO availability on fish consumption in our GRP models. By contrasting these estimates

of habitat quality (estimated by GRP) with those from our normal model, which included a DO effect on consumption, we could evaluate the independent effect of bottom hypoxia on habitat quality for both species (see Supplemental Information[1]).

Fish hydroacoustics, trawling, and abundance estimation

Relative fish biomass was measured with a Biosonics (Seattle, Washington) DTX split-beam echosounder (frequency = 120 kHz, pulse duration = 0.4 ms, ping rate = 4 pings·s⁻¹, acquisition threshold = –66 dB re 1 μPa) that was towed simultaneously with the PSS at ~2.5 m·s⁻¹. The transducer was towed 1–2 m below the surface, depending on surface wave conditions, thus potentially causing us to underestimate near-surface biomass, as emerald shiners tend to school at the water's surface during the daytime (Trautman 1981). We conducted calibrations with a 38-mm tungsten–carbide sphere on every cruise and used S_v (dB re 1 m⁻¹) as a relative measure of fish biomass density (Simmonds and MacLennan 2006), wherein higher levels of S_v correspond to higher levels of total fish biomass density (Taylor et al. 2007; Ludsin et al. 2009). Acoustics data were processed using Echoview (SonarData Inc., Hobart, Tasmania), with volume backscattering strength (S_v; units of dB, a logarithmic measure of s_v) exported in 50 × 1 m bins. Additional details about the fish acoustics can be found in Vanderploeg et al. (2009a).

Fish trawls were conducted at the ends of short diel transects (Fig. 2) every 4 h over a 24-h period during August, September, and October 2005. Fish were captured using a 7.6-m semiballoon bottom trawl (13-mm stretched-mesh cod liner) and a 9.1 m × 9.1 m midwater trawl (6.4-mm stretched-mesh cod liner). Each trawl was towed for 10 to 20 min at the 5-km diel station, with a minimum of one bottom and one midwater trawl conducted during every 4-h interval. Fish were sorted by species and immediately placed in a –20 °C freezer. Trawl data are reported as CPUE (number of individuals per trawl minute).

We used acoustics (proportional s_v) data to estimate the abundance of fish (number of individuals·ha⁻¹) in different layers of the water column during August, September, and October 2005, following the methods described in Pothoven et al. (2012). During August and September, when the water column was thermally stratified, we estimated the proportion of fish abundance in the epilimnion, metalimnion, and hypolimnion. Because October sampling occurred ~7 days after the water column remixed (i.e., destratified), we estimated the proportion of fish abundance in the upper half and lower half of the water column. To explore where fish moved horizontally in relation to hypoxia, we measured the acoustic backscatter of fish targets along multiple transects that spanned the hypoxic zones of 2005 and 2007. To do so, we averaged the area backscattering coefficient (ABC; m²·m⁻²) in the hypolimnion at regular intervals (~1 km) along these transects and then plotted values on top of observed hypolimnetic DO levels.

Fish consumption, growth, and energetic condition

Only rainbow smelt and emerald shiners captured at diel station B during 2005 were analyzed for this study. In the laboratory, all individuals were thawed, measured (nearest 1 mm total length, TL), and weighed (nearest 0.01 g wet weight). Stomach contents were then removed, and the entire fish (minus stomach contents) was dried at 70 °C to a constant mass (nearest 0.0001 g). We assessed fish energetic condition by dividing each individual's dry weight by its corresponding wet weight, as our own data (S.A. Pothoven, unpublished data) and previous research has shown this dry:wet weight ratio to be strongly, positively correlated with energy density (Pothoven et al. 2006; Morley et al. 2012). In this way, individuals with a higher dry:wet mass ratio (i.e., higher energy density) can be considered in better energetic condition than those with a lower ratio.

We analyzed the stomach contents of a subsample of adult fish collected during each diel period. These samples were initially

analyzed by Pothoven et al. (2009) as part of a broader dataset. The dataset analyzed herein was constrained to the same site where acoustics data were collected to better identify the effects of hypoxia on catches, diet, length, and condition metrics. In brief, we subsampled individuals from larger catches until we achieved about 25 individuals (per species per 4-h interval) with food in their stomachs (if available). For rainbow smelt, only age 1+ (>70 mm) individuals were used for analysis because few age 0 individuals were caught. For emerald shiners, individuals greater than 70, 75, and 80 mm were classified as adults for August, September, and October, respectively. Our ability to discern adult fish was facilitated by age 0 individuals also being collected. For both species, after we processed diets, we dried the stomach contents at 70 °C to a constant mass (nearest 0.0001 g), which allowed us to estimate individual mass-specific consumption.

We identified, measured, and counted both zooplankton and benthic macroinvertebrates in the guts of fish following Pothoven et al. (2009). All large prey (e.g., Chironomidae pupae and larvae; *Bythotrephes longimanus*; *Leptodora kindtii*) from each stomach were identified and counted. Head capsules (Chironomidae) or bodies with eye-spots (*B. longimanus*, *L. kindtii*) were used to count partial prey. Bodies were used to provide a conservative estimate of *B. longimanus* because spines can accumulate in stomachs (Parker et al. 2001). Mesozooplankton (e.g., Copepoda, Cladocera) from each stomach were added to a known volume (10–25 mL) of water and subsampled with a 1-mL aliquot so that at least 100 individuals were counted. If stomachs contained fewer than 100 mesozooplankton, all individuals were counted. Mesozooplankton was classified as Bosminidae, Daphniidae, Sididae, Chydoridae, Cyclopoida, Calanoida, and Copepoda nauplii.

To determine the biomass of prey consumed, prey lengths of up to 20 intact individuals of each prey group (except nauplii) were measured using ImagePro image analysis software (Media Cybernetics, Silver Spring, Maryland). Prey length was converted to dry mass using mass–length regressions (Culver et al. 1985; Makarewicz and Jones 1990; S.A. Pothoven and T. Nalepa, University of Michigan, Lansing, Michigan, unpublished data). The average dry mass of an individual of each prey type was determined for each size class of fish for each site and month and multiplied by the number of each prey type in a stomach to determine dry biomass contribution of each prey type in an individual stomach.

We used one-way analysis of variance (ANOVA) and post hoc Tukey's honestly significant difference tests to quantify differences in the catch, consumption, body mass, and energetic condition (energy density) of both rainbow smelt and emerald shiners before (August), during (September), and immediately after (October) peak hypoxia. All data met assumptions of normality and homogeneous variances. An alpha value was set to 0.05 for all analysis.

Long-term population trends

To explore the effect of hypoxia on the rainbow smelt and emerald shiner populations at large in Lake Erie's central basin, as well as the effect of hypoxia severity on commercial catchability of rainbow smelt, we relied on long-term (1986–2014) time-series data. Because rainbow smelt and emerald shiners are preferred prey items of walleye in Lake Erie (Knight et al. 1984; Knight and Vondracek 1993; Madenjian et al. 2018), we also explored the effect of walleye abundance as a confounding factor of fish population change. We calculated a relative hypoxia severity index using DO data from the USEPA Great Lakes Environmental Database (GLENDA; http://www.exchangenetwork.net/data-exchange/glenda/). These data consisted of bottom DO concentrations (nearest 0.1 mg·L⁻¹) from 10 sites sampled during August throughout the central basin of Lake Erie during 1986–1991 and 1996–2014. Hypoxic extent during each year was interpolated using an inverse-distance weighted method in ArcGIS 10.5 (ESRI, Redlands, California, USA), and the percentage of the interpolated area with bottom DO < 4 mg·L⁻¹ was calculated to create an index of hypoxia severity. Rainbow

Fig. 3. Daytime survey data collected in central Lake Erie along "long" transect B during August, September, and October 2005. Observed temperature (panels A, G, and M), dissolved oxygen (DO; panels B, H, and N), and zooplankton biomass (panels C, I, and O) collected by a plankton sampling system (PSS) were used to estimate the growth rate potential (GRP, g·g^{-1}·day^{-1}) of emerald shiners (panels D, J, and P) and rainbow smelt (panels E, K, and Q). Observed acoustic backscatter data (S_v, log scale) measured throughout the water column simultaneously with the PSS data are presented as relative fish biomass (panels F, L, and R). Transects were surveyed from the south (left) to north (right). The lake bottom is displayed in grey.
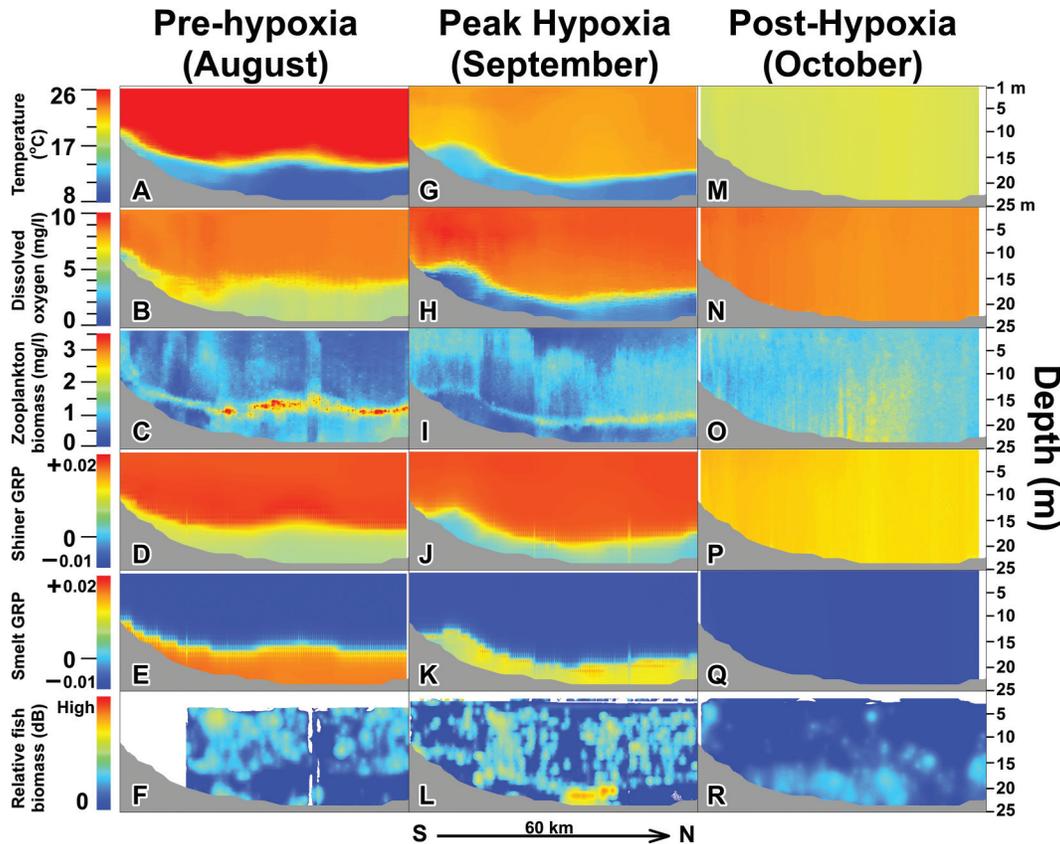
smelt and emerald shiner fishery-independent catch data from fall (late September through early October) assessment surveys conducted in the central basin of Lake Erie were provided by the Ohio Department of Natural Resources – Division of Wildlife (ODNR–DOW 2018). Total annual Lake Erie walleye population sizes were obtained from the Great Lakes Fishery Commission – Lake Erie Walleye Task Group (Wills et al. 2018). Spatially explicit (10 min × 10 min grids) commercial fishing catch and effort data for rainbow smelt in Canadian waters during 1998–2014 were provided by the Ontario Ministry of Natural Resources and Forestry. We calculated a CPUE for each fishing occurrence, as well as a mean CPUE during August for each year.

To help determine whether hypoxia severity influenced the demographics of rainbow smelt and emerald shiners during 1986–2014, we used both univariate and multiple linear regression approaches. As a first step, we correlated rainbow smelt and emerald shiner fishery-independent estimates of abundance during fall, as well as rainbow smelt CPUE in commercially fished trawls (during August), to our index of hypoxia severity and observed walleye population size. Our indices of hypoxia severity and walleye population size were calculated as a running 3-year average (i.e., average of summer conditions during the current year and the previous 2 years), as the majority of rainbow smelt and emerald shiners captured annually by the ODNR–DOW during 1986–2014 were age 2 or older (i.e., individuals had lived at least three summers; S.A. Ludsin, unpublished data), and this 3-year average is more indicative of the cumulative conditions experienced by the fish over its lifetime than just a single-year hypoxic event.

Finding that rainbow smelt abundance was strongly correlated with both hypoxia severity and walleye population size, we used multiple linear regression to assess their combined influence on rainbow smelt abundance. Hypoxia severity and walleye population size were uncorrelated ($r = 0.11$), justifying the inclusion of both variables, as well as their interaction, in our multiple regression analysis. We used the Akaike information criterion for small sample sizes (AIC$_c$; Burnham and Anderson 2002) to determine the most parsimonious predictive model(s) of rainbow smelt CPUE. This analysis tested all models from the simplest (intercept only) to the most expansive (both independent predictors, their interaction, and the intercept). Models with an AIC$_c$ < 2 were considered equally as probable (Burnham and Anderson 2002).

Normality and linearity of all data were assessed before analysis. Non-normal data (rainbow smelt and emerald shiner abundances) were log$_{10}$-transformed to meet assumptions of normality. The alpha value was set to 0.05 for all analyses, with a Bonferroni adjustment made to the P value when multiple comparisons were conducted.

Results

Habitat quality and fish distributions

August 2005 (pre-hypoxia)

High-quality habitat for both emerald shiners and rainbow smelt, as evidenced by positive GRP values, existed along transect B during August (Figs. 3A–3F). The water column was thermally stratified along this transect, with the thermocline being located ~9 m off the lake bottom (Table 2; Fig. 3A). The hypolimnion was

Table 2. Mean (±1 standard deviation) water temperature, dissolved oxygen concentration (DO), and zooplankton biomass in each water column layer at diel station B in central Lake Erie during August, September, and October 2005.

Month	Layer	Depth range (m)	Temperature (°C)	DO (mg·L⁻¹)	Zooplankton (mg·L⁻¹)
August	Epilimnion	0.0–12.8	25.0±0.9	8.7±0.5	0.8±0.2
	Metalimnion	12.8–14.0	15.9±2.7	6.2±0.5	1.4±0.2
	Hypolimnion	14.0–23.2	10.0±0.3	4.8±0.3	0.7±0.3
September	Epilimnion	0.0–16.8	21.9±0.1	8.4±0.6	1.0±0.1
	Metalimnion	16.8–17.1	17.2±2.7	4.8±1.1	1.7±0.4
	Hypolimnion	17.1–23.2	11.1±0.2	1.7±0.8	0.8±0.3
October	Upper	0.0–11.6	18.8±0.1	7.8±0.3	1.2±0.4
	Lower	11.6–23.2	18.8±0.1	7.8±0.2	0.8±0.1

Note: Data were collected by a plankton sampling system and averaged across the entire length of the 5-km station for each layer of the water column.

not yet hypoxic, with DO levels ≥ 4 mg·L⁻¹ at all depths (Table 2; Fig. 3B). Zooplankton biomass was highest offshore and in the metalimnion, which included the thermocline region (Table 2; Fig. 3C). While emerald shiner GRP was positive throughout the water column during August, it was highest near the thermocline and in the warm epilimnion (Fig. 3D). By contrast rainbow smelt GRP during August was positive only in the cold hypolimnion (Fig. 3E). Daytime acoustic survey data revealed that fish biomass was widely distributed along transect B during August, with levels being relative higher above the thermocline than below it, although some fish aggregations were detected in the hypolimnion (Fig. 3F).

September 2005 (peak hypoxia)

High-quality habitat decreased during September along transect B for both species, especially for rainbow smelt (Figs. 3G–3L). Similar to August, the water column was stratified during September (Fig. 3G); however, hypolimnetic hypoxia (DO < 3 mg·L⁻¹) was now present across nearly the entire transect (Table 2; Fig. 3H). Similar to August, zooplankton biomass was highest in the offshore metalimnion, which encompassed the thermocline (Table 2; Fig. 3I). Even so, zooplankton biomass was lower in both the hypolimnion and thermocline regions compared with August, with zooplankton biomass instead being more widely distributed in the warm, oxygenated epilimnion during September (see Figs. 3C, 3I). While emerald shiner GRP was again positive in the thermocline and epilimnion, it approached zero in the hypolimnion, unlike during August (Fig. 3J). By contrast, rainbow smelt GRP was only positive in the hypolimnion (with lower values than during August; see Fig. 3E), completely negative in the epilimnion, and slightly higher near the thermocline (Fig. 3K). Fish detected acoustically were evenly distributed throughout the epilimnion and largely absent in most areas of the hypoxic hypolimnion, with the exception of a large aggregation found offshore (Fig. 3L) in an area with slightly elevated DO relative to the surrounding areas (see Fig. 3H and Fig. 7, top panel).

October 2005 (post-hypoxia)

During October, habitat quality varied considerably between the two species. No stratification was present, as sampling occurred ~7 days after the lake remixed, with the entire water column being ~19 °C and having ~8 mg O₂·L⁻¹ (Figs. 3M, 3N). Zooplankton biomass was highest in offshore waters (Fig. 3O). Emerald shiner GRP was uniformly positive across the transect (Fig. 3P), and rainbow smelt GRP was uniformly negative throughout the entire water column (Fig. 3Q), as temperatures exceeded this species' suggested lethal limit of 20 °C (Lantry and Stewart 1993). Relative fish biomass was lower compared with August or September, with fish mostly concentrated in offshore bottom waters (Fig. 3R).

September 2007 (hypoxia)

We also calculated GRP for transect D during September 2007 from measured temperature and DO and estimated zooplankton biomass. Transect D began in the eastern central basin and terminated at Clear Creek Ridge, a shallow, north–south ridge that separates the central and eastern basins of Lake Erie (see Fig. 2, bottom panel). Stratification was present along the transect until Clear Creek Ridge, where the bottom depth was close to the depth of the thermocline (~16 m; Fig. 4A). Hypolimnetic waters were hypoxic (<3 mg O₂·L⁻¹) in the western portion of the transect, with bottom DO increasing towards the east and approaching 4 mg O₂·L⁻¹ on Clear Creek Ridge (Fig. 4B). Emerald shiner GRP was positive throughout the entire water column, being higher in the epilimnion than in the hypolimnion (Fig. 4C). By contrast, rainbow smelt GRP was negative in the entire epilimnion and positive in the hypolimnion, with GRP values increasing in the hypolimnion towards Clear Creek Ridge, located on the eastern part of the transect (Fig. 4D). Relative fish biomass, measured acoustically, was highest in the hypolimnion in the eastern part of the transect near Clear Creek Ridge (Fig. 4E), where GRP values were also high (see Fig. 4D). Smaller aggregations of fish biomass were located higher up in the water column (Fig. 4E).

Fish vertical distribution

To explore how hypoxia influences the vertical distribution of fish in the water column, we relied on acoustic surveys and trawling conducted at the short (5 km) diel station located near the midpoint of the longer transect B (see Fig. 2, top panel) during August, September, and October 2005 (see Table 2). During pre-hypoxic conditions in August, fish were abundant in the hypolimnion, based on the proportional distribution of acoustic backscatter (s_v) across the 5-km station (Fig. 5A). During September, when hypoxia was well-developed, fish were absent in the hypolimnion and aggregated mostly in the thermocline region just above the hypoxic layer (Fig. 5B). After stratification and hypoxia ended during early October, fish were evenly distributed throughout the water column (Fig. 5C).

Analysis of bottom and midwater trawl catch data collected simultaneously with the acoustic surveys at diel station B revealed species-specific differences in vertical distribution across the growing season (Fig. 6A). During the pre-hypoxic period (August), rainbow smelt comprised 93% of the bottom trawl catch (by abundance). During peak hypoxia (September), no rainbow smelt (0%) were caught in bottom trawls. However, once stratification ended in October, fish were distributed between the lower and upper layers of the water column (68% in bottom trawls). For emerald shiners, no significant differences in vertical distribution were found for any month. However, as with rainbow smelt, no emerald shiners were caught in the bottom trawls during hypoxia, as

Fig. 4. Daytime survey data collected in the eastern part of central Lake Erie along "long" transect D during September 2007. Observed temperature (A) and dissolved oxygen (DO; B) collected by a plankton sampling system (PSS) were used to estimate the growth rate potential (GRP, g·g⁻¹·day⁻¹) of emerald shiners (C) and rainbow smelt (D). Observed acoustic backscatter data (S_v, log scale) measured throughout the water column simultaneous with the PSS data are presented as relative fish biomass (E). Owing to our optical plankton counter (OPC) on the PSS failing, a constant, estimated zooplankton biomass was used in each cell when calculating GRP (see Appendix A). The transect was surveyed from the west (left) to east (right). The lake bottom is displayed in grey.
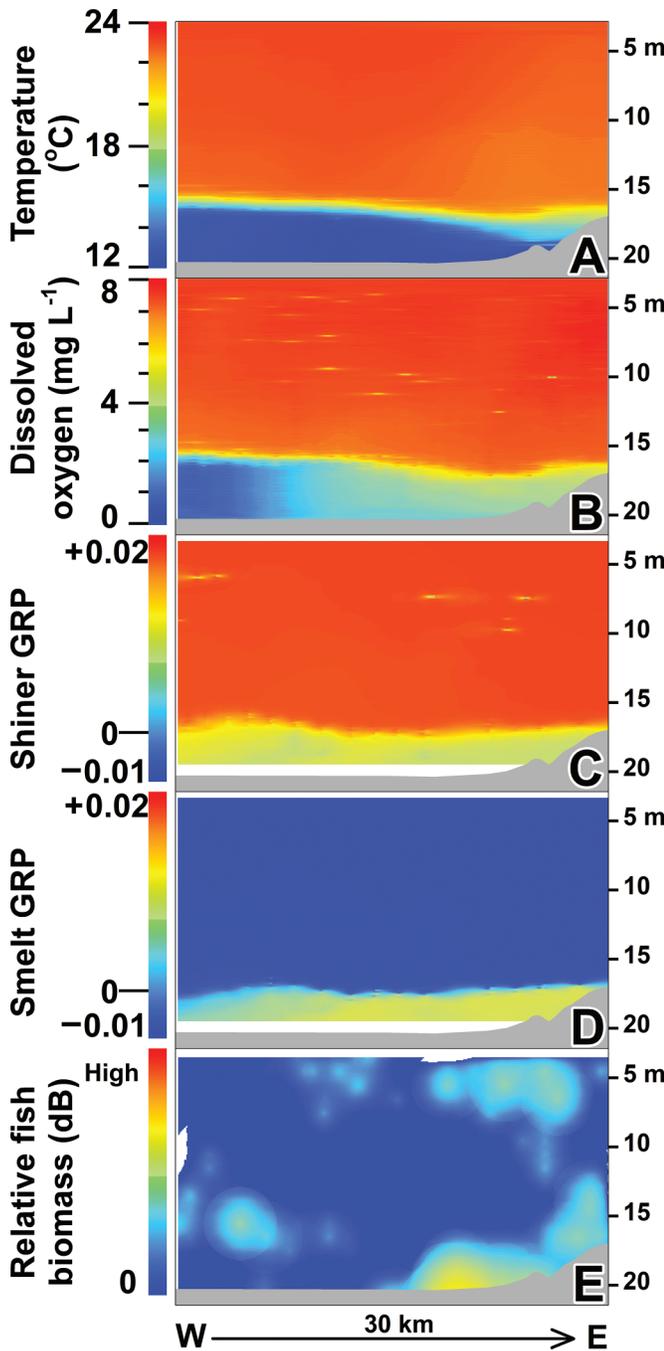
Fig. 5. Daytime vertical distribution of fish in central Lake Erie at diel site B, located near the midpoint of the longer transect B during August (A, pre-hypoxia), September (B, peak hypoxia), and October (C, post-hypoxia) 2005. Mean proportion of total abundance (number of individuals·ha⁻¹) in each water column stratum was calculated from fish hydroacoustics (proportional s_v). Water column strata were determined based on the thermocline position during August and September (upper = epilimnion; middle = metalimnion; lower = hypolimnion) and at the midpoint of the water column in October, as no thermocline was present (see Table 2). Error bars represent one standard deviation.
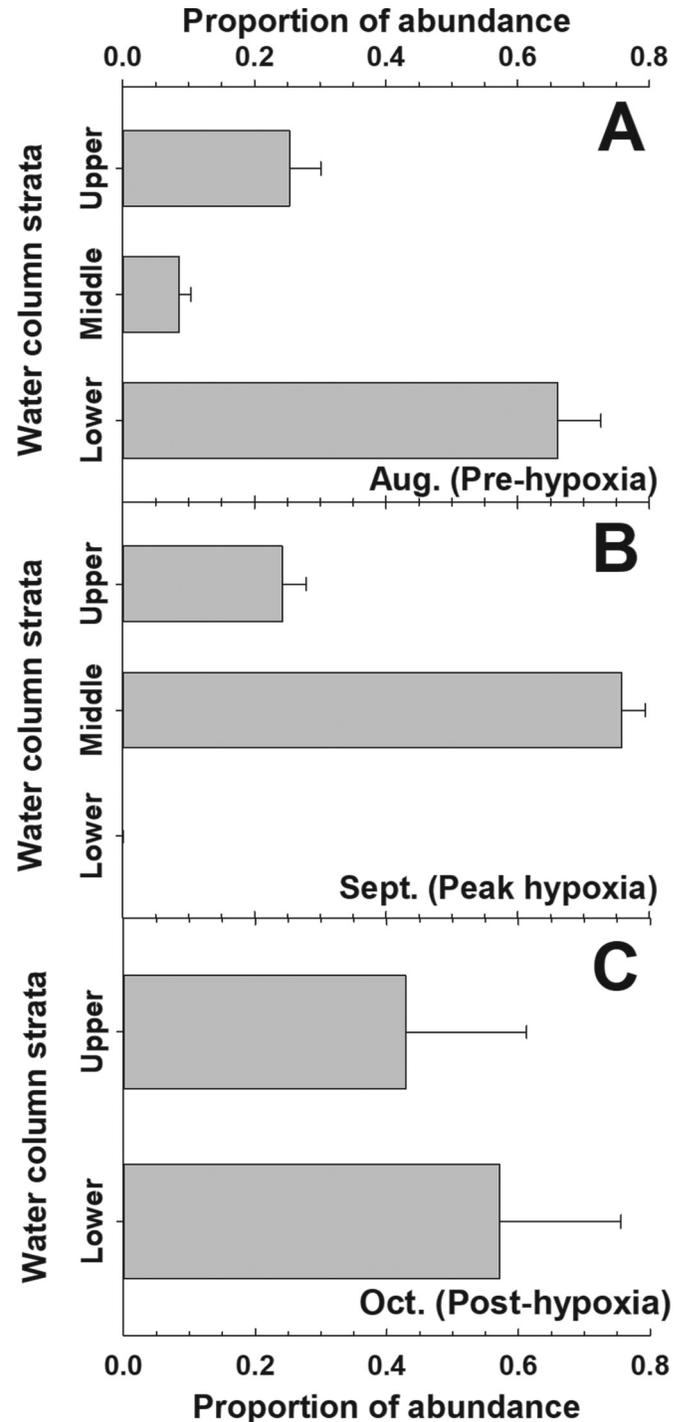
Fig. 6. Comparison of rainbow smelt (left bars) and emerald shiner (right bars) attributes in central Lake Erie (at diel station B) during August (pre-hypoxia), September (peak hypoxia), and October (post-hypoxia) 2005. Fractional catches (based on abundance) in bottom trawls (i.e., vertical distribution; A), mean mass-specific total diet biomass ($g_{diet\ mass} \cdot g_{fish\ mass}^{-1}$; B), proportional biomass of benthic prey items in the diet (C), mean total length (mm; D), and mean energetic condition (i.e., estimated energy density represented by ratio of fish dry weight (g) to wet weight (g); E). Fish catches, diet content, and body size and condition were compared among months using one-way ANOVAs. Months with no letters in common (for a species within a panel) are significantly different ($\alpha = 0.05$) based on post hoc Tukey's honestly significant difference tests. Error bars represent one standard error.
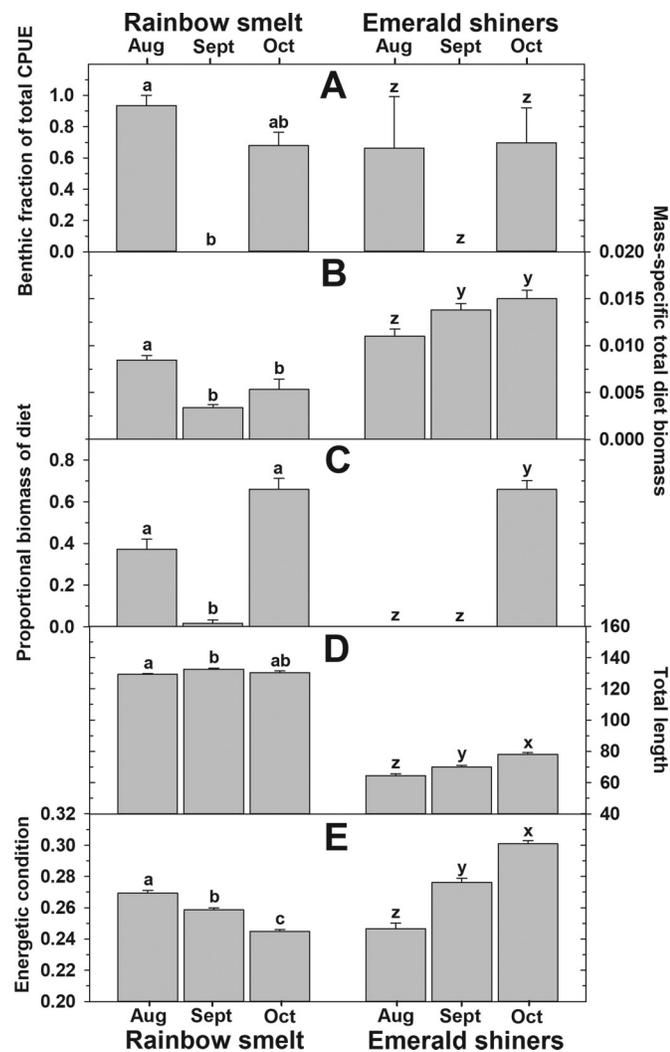
opposed to making up 66% and 70% of the catch from the bottom trawls during August and October, respectively (Fig. 6A).

Fish diet biomass

To quantify the impact of hypoxia on rainbow smelt and emerald shiner prey consumption, we analyzed the stomach contents of both species collected before (August), during (September), and immediately after (October) the hypoxic period in 2005. For rainbow smelt, mass-specific gut content was significantly higher during August than during September or October (Fig. 6B), and the benthic fraction of the diet was significantly lower during the hypoxic period (2%) than before or immediately after it (37% and 66%, respectively; Fig. 6C). By contrast, the mass-specific gut con-

tent of emerald shiners increased from August into September and October (Fig. 6B), and the benthic fraction of the diet was 0% during stratification (August and September) and significantly higher (66%) after stratification ended (October; Fig. 6C). A large portion of the benthic organisms consumed by emerald shiners in October were Chironomidae larvae and emerging pupae (Pothoven et al. 2012).

Fish growth and energetic condition

For both emerald shiners and rainbow smelt, we evaluated their size and energetic condition during the pre-hypoxic (August), hypoxic (September), and post-hypoxic (October) periods. Rainbow smelt TL only increased during the pre-hypoxic period (from August into September) and remained unchanged from September into October, which encompassed the hypoxic period and only ~7 days afterwards (Fig. 6D). Rainbow smelt energy density, as proxied by the dry weight to wet weight ratio, significantly decreased with each successive month (Fig. 6E). Opposite patterns were found for emerald shiners with both TL (Fig. 6D) and energy density (Fig. 6E), both of which significantly increased in each successive month during the summer growing season, despite the presence of hypolimnetic hypoxia.

Fish horizontal distribution

The plot of hypolimnetic fish abundance and DO (Fig. 7) shows some aggregation of fish in pockets of slightly higher DO within the hypoxic zone (e.g., near 42°N, 81°45′W in 2005), but mostly fish aggregating at the edges of the hypoxic zone, which covered most of the area surveyed (Fig. 7). To further understand how hypoxia might be driving fish aggregations, we explored how hypolimnetic fish biomass (using ABC as a proxy) varied with hypolimnetic DO concentration in different areas of the hypoxic zone (outside of it, at the edge of it, inside of it) during both years. During 2005, fish biomass in the hypolimnion outside of the hypoxic zone (where bottom DO > 2 mg·L^{-1}) was significantly higher at a bottom DO of 2.25–2.75 mg·L^{-1} relative to other DO concentrations (Fig. 8A). At the edge of hypoxic zone (within 4 km of the 2 mg·L^{-1} isopleth), fish biomass was highest at 2.75–3.25 mg·L^{-1} (Fig. 8C). A similar distributional pattern was observed during 2007, when fish had significantly higher biomass in the hypolimnion at bottom DO concentrations of 3.25–4.25 mg·L^{-1} outside of the hypoxic zone (Fig. 8B) and 2.75–3.25 mg·L^{-1} at the hypoxic edge (Fig. 8D). During both years, fish biomass inside the hypoxic zone (bottom DO < 2 mg·L^{-1}) was low, and fish biomass did significantly vary with bottom DO concentration (Figs. 8E–8F).

Long-term population trends

We examined the effects of bottom hypoxia severity on fisheries-independent estimates of rainbow smelt and emerald shiner abundance during 1986–2014. The fall abundance of central basin rainbow smelt was negatively correlated with the areal extent of bottom hypoxia severity (areal extent of hypoxia; Fig. 9A), as well as the size of the adult walleye population (Fig. 9B). Additionally, multiple linear regression modeling showed that both variables (hypoxia severity, walleye population size) were important predictors of rainbow smelt abundance, each explaining unique variation in their abundance (Table 3). Overall, our most parsimonious model (see Table S1[1]), which included both variables, explained 49% of the variation in rainbow smelt abundance, with the variation being equally split between the two variables (Table 3). Central basin adult emerald shiner abundance was also negatively correlated with bottom hypoxic area (Fig. 9C), but was unrelated to walleye population size (Fig. 9D).

We also investigated the potential influence of bottom hypoxia on rainbow smelt catches by commercial fishers in Ontario waters of central Lake Erie during 1998–2014. Our analyses showed that rainbow smelt (fisheries-dependent) catches during August were significantly, positively correlated with the areal extent (severity)

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Fig. 8. Horizontal distribution of fish biomass relative to the hypoxic zone in central Lake Erie during 2005 and 2007. The hypolimnetic area backscattering coefficient (ABC, proxy for fish biomass) was averaged for each bottom dissolved oxygen (DO) bin (in 0.5 mg·L⁻¹ intervals) across all acoustic transects sampled during September 2005 and 2007. Black dots indicate average ABC, whereas gray bars indicate the percentage of the surveyed area represented by that bin. Surveyed areas are divided by their proximity to the 2 mg·L⁻¹ DO isopleth into regions outside (A, B), at the edge of (C, D), and inside (E, F) the hypoxic zone, with the edge consisting of any area within 4 km of 2 mg·L⁻¹ bottom DO. Error bars represent one standard deviation; asterisks indicate a significant difference ($\alpha = 0.05$) in pairwise comparisons (t tests) with more than two other bins.
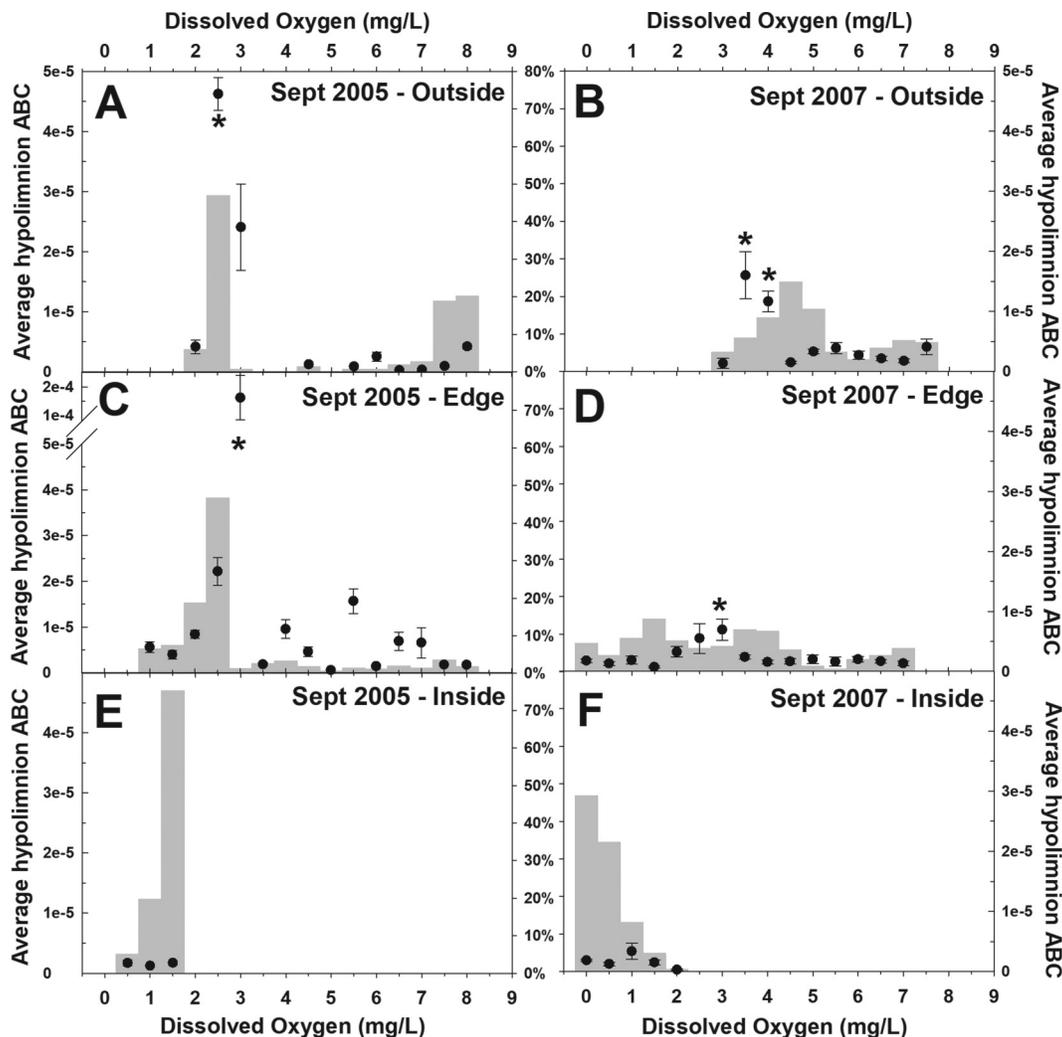
the (hypoxic) bottom layer during the daytime, instead residing above this layer near the oxygenated thermocline. For example, along our repeatedly sampled diel station along transect B, which had an area of low GRP, acoustically surveyed fish biomass was higher in the hypolimnion before hypoxia occurred, whereas during the hypoxic period, fish biomass was closer to the thermocline (Vanderploeg et al. 2009*b*; see Fig. 5). Trawl data agreed with the acoustic surveys (see Fig. 6A) and demonstrated that this vertical movement of fish was primarily due to movement of rainbow smelt (also see Pothoven et al. 2009). These results support previous studies that have demonstrated altered DVM behavior in planktivorous fishes in the presence of hypoxia, with fish ceasing migrations into bottom waters in Lake Erie (MacCullum and Regier 1970; Vanderploeg et al. 2009*b*; Pothoven et al. 2012) and elsewhere (e.g., Neuse River Estuary: Taylor et al. 2007; Chesapeake Bay: Ludsin et al. 2009; northern Gulf of Mexico: Zhang et al. 2009).

Emerald shiners were not present in bottom trawls during hypoxia; however, this absence was not statistically different from their vertical distributions before or after hypoxia, which conforms with their known preference for warm surface water during summer

(McCormick and Kleiner 2002). While the mechanisms underlying their use of the epilimnion are unknown, we perceive this behavior as an evolved behavioral response to predation risk, as foraging by central Lake Erie's **native** top predators in surface waters are limited by temperature (in the case of burbot and lake trout; Maclean et al. 1981; Hoffman and Fischer 2002) or high light levels (in the case of walleye; Ryder 1977, Lester et al. 2004). Alternatively, this daytime use of the epilimnion could be an evolved response to bottom hypoxia, which is thought to be a natural phenomenon in central Lake Erie (Delorme 1982).

Horizontal distribution

Fish also moved horizontally to avoid bottom hypoxia. As a result, rainbow smelt occupied small pockets of slightly higher habitat quality that existed in the thin metalimnetic layer, as well as in the hypolimnion where DO was slightly higher than the surrounding waters (~0.25 mg·L⁻¹; e.g., along transect B in the deepest part of the central basin; see Fig. 7, top panel). This phenomenon also is evident in the cross-sections of transect B during September 2005 and transect D during September 2007, where fish in the hypolimnion were less dispersed than other months

Fig. 9. Relationships between rainbow smelt and emerald shiner abundance and bottom hypoxia severity and walleye population size in central Lake Erie. Adult rainbow smelt (A, B) and adult emerald shiner (C, D) abundances are the mean central basin catch per unit effort (CPUE; number of individuals per trawl minute) in late fall (post-hypoxia) fisheries-independent trawl surveys conducted during 1986–1991 and 1996–2014. These abundances were correlated to the 3-year running mean of central basin bottom hypoxic extent (A, C; percentage of USEPA–GLNPO coverage area with <3 mg $O_2 \cdot L^{-1}$) and 3-year running mean of Lake Erie age 2+ walleye population size (B, D). Pearson's r correlation statistics are reported with the least-squares regression line plotted. Abundances were natural log-transformed to meet assumptions of normality. No DO data existed during 1992–1995.
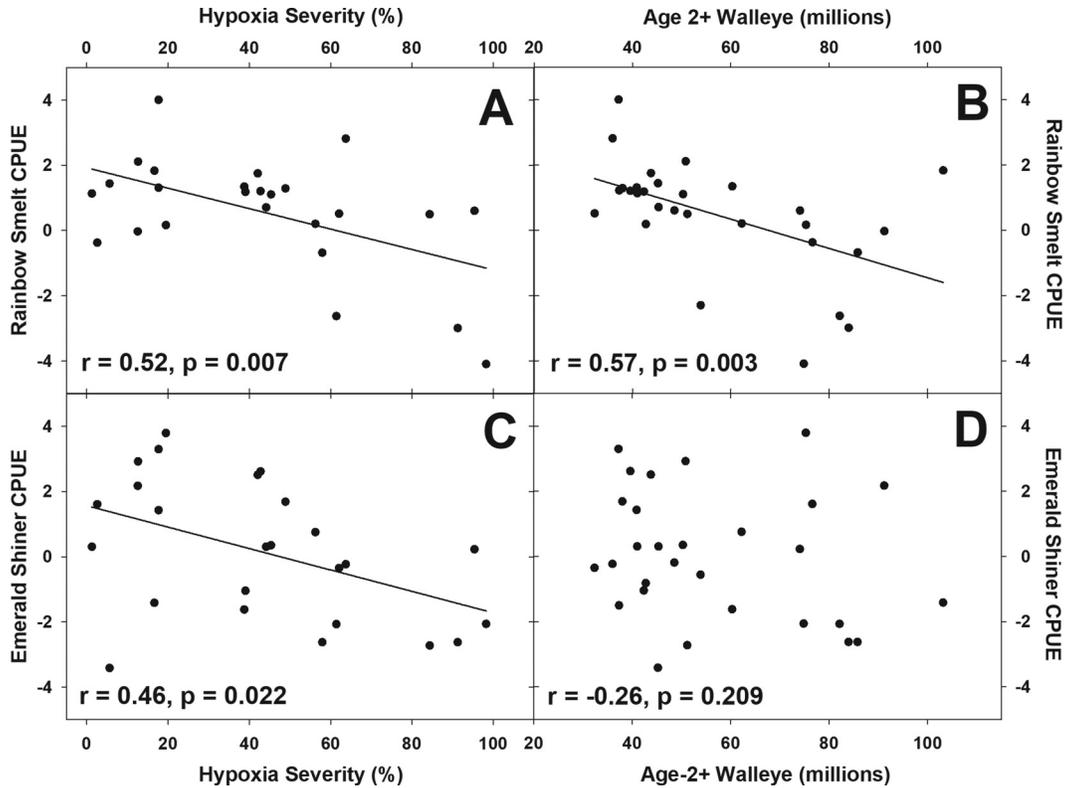

Table 3. Results of a multiple linear regression used to predict fishery-independent age 2+ rainbow smelt catch per unit effort (number of individuals per trawl minute) in central Lake Erie during 1986–2014 from the severity of hypoxia (percentage of central basin with dissolved oxygen < 4 mg·L^{-1}) and the estimated population size of adult (age 2+) walleye in the lake ($R^2 = 0.49$, $p < 0.001$).

Model variable	Coefficient estimate	Coefficient SE	P
Intercept	4.34	0.822	<0.001
Hypoxia severity	-2.78×10^{-2}	8.77×10^{-3}	0.004
Walleye population size	-4.38×10^{-8}	1.25×10^{-8}	0.002

Note: This model was deemed the most parsimonious based on AIC$_c$ analysis (Table S1[1]). Three-year running averages of hypoxia severity and walleye abundance were used, as the rainbow smelt collected by trawls were predominantly age 2+ (i.e., individuals potentially experienced three summers of hypoxia and predation pressure). Plots of the raw data used in this analysis can be found in Fig. 1.

and aggregated in areas of the highest GRP and correspondingly high DO (see Figs. 7 and 8). Interestingly, fish in the hypolimnion were most concentrated in areas within a narrow range of DO conditions.

Rainbow smelt likely sought out areas of low temperature (10–12 °C) and the highest DO possible in that temperature range, which are the areas of highest GRP. The ranges of ideal DO and temperature appear to depend on the severity of hypoxia, as the range observed was 2.25–3.25 mg·L^{-1} during 2005 and 2.75–4.25 mg·L^{-1} during 2007. This pattern held true whether individuals were at the edge of the hypoxia zone (within 4 km of the

Fig. 10. Correlation between rainbow smelt commercial catches and hypoxia severity in central Lake Erie, 1998–2014. Mean August commercial catch per unit effort (CPUE) of rainbow smelt in Canadian waters is plotted against the percentage of the central basin bottom waters surveyed by US Environmental Protection Agency that is <4 mg $O_2 \cdot L^{-1}$ for each year. Pearson's r correlation statistic is reported with the least-squares regression line plotted.
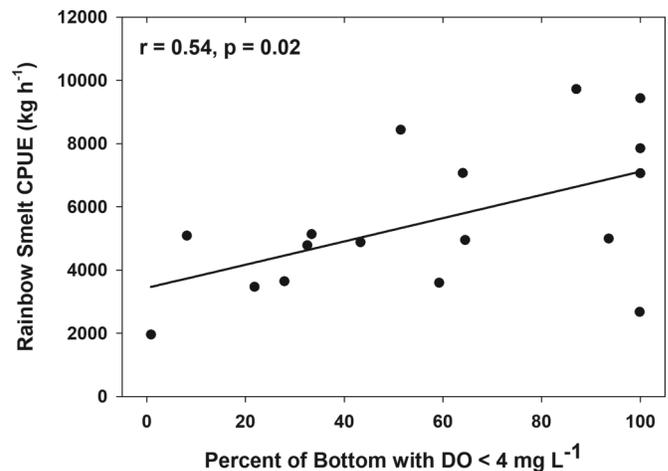
2.0 mg·L^{-1} isopleth) or completely outside of the hypoxia zone (>4 km from an area of 2.0 mg·L^{-1} or less). If individuals were trapped well within the hypoxic zone (farther than 4 km from an area of 2.0 mg·L^{-1} or greater), they showed no preference for

higher hypolimnetic DO within the 0.5–2.0 mg·L^{-1} range. This finding of variable tolerances of hypoxia has been shown in both the Neuse River estuary (Eby and Crowder 2002), as well as the northern Gulf of Mexico (Zhang et al. 2014). In general, the threshold level of DO avoidance increases with decreasing hypoxia extent (Eby and Crowder 2002).

Short-term effects of hypoxia on fish performance

Prey consumption

The hypoxia-induced exclusion of fish from the hypolimnion led to changes in the prey types consumed by rainbow smelt and emerald shiners, a finding that has been previously documented in central Lake Erie (Pothoven et al. 2009). By excluding adult rainbow smelt from the hypolimnion, hypoxia reduced their access to benthic prey items that made up a substantial portion of their diet during the pre- and post-hypoxic periods. Emerald shiners also did not feed on benthic prey during stratification (either pre- or peak hypoxia), a period when the hypolimnion had lower habitat quality than the epilimnion. However, once stratification ended, benthic items became a major portion of emerald shiner diets, although we suspect that this diet shift was facilitated by a chironomid midge hatch that occurred during our sampling (S.A. Pothoven and S.A. Ludsin, personal observation).

Reductions in mass-specific total diet biomass also reflect the exclusion of rainbow smelt from the hypolimnion during hypoxia. When bottom hypoxia is present, rainbow smelt likely compete more directly with emerald shiners for prey than before or afterwards (Pothoven et al. 2009, 2012). Indeed, rainbow smelt stomach biomass was significantly lower during the hypoxic period than prior to it, which was not the case for emerald shiners (see Fig. 6). In addition to competing for zooplankton with emerald shiners, rainbow smelt may also have experienced reduced consumption during the hypoxic period because of physiological stress caused by warmer than optimal water temperature (Lantry and Stewart 1993).

Growth and energetic condition

The influence of hypoxia on growth and energetic condition (estimated energy density) differed between rainbow smelt and emerald shiners. The average length of rainbow smelt failed to increase during the hypoxic period, whereas emerald shiner length increased during the same period. In addition, while the energetic condition of emerald shiners increased throughout the summer into fall, as expected, rainbow smelt condition decreased from August to September and again from September to early October. Because assessment of somatic growth and energetic condition only occurred during one year, the possibility exists that this trend is a normal pattern and is unrelated to hypoxia. However, this decrease in rainbow smelt energetic condition (energy density) came at a time (end of summer) when we would expect it to increase in preparation for the winter, a season when food resources are scarce. Indeed, rainbow smelt energy density has been shown to increase with age or remain stable in other Great Lakes rainbow smelt populations during summer into fall, with the only reductions occurring postspawning during the spring (Foltz and Norden 1977; Rand et al. 1994).

We strongly believe that this reduction in rainbow smelt somatic growth and energetic condition resulted from physiological stress caused by a combination of high temperature (Lantry and Stewart 1993), low DO (Hanks and Secor 2011), and reduced feeding during hypoxia. The near-lethal temperatures that occurred throughout the entire water column after fall mixing would be expected to have strong negative effects on the growth and energetic condition for adult, as well as yearling (see Table S2[1]), rainbow smelt that are unable to escape horizontally. Given that both water temperature and bottom hypoxia are expected to increase in Lake Erie with continued climate change (Bosch et al. 2014; Scavia et al. 2014; Rucinski et al. 2016), we suspect that habitat

suitability will only continue to decrease during the summer growing season.

Even if fish are able to escape from hypoxic bottom waters into more oxygenated waters, this movement behavior and distributional shift can have short-term negative consequences. For example, hypoxia-induced movement has been shown to increase energetic expenditures by zooplanktivorous bay anchovy in the Neuse River (Taylor and Rand 2003; Taylor et al. 2007). Likewise, Craig and Crowder (2005) showed that hypoxia avoidance increased energy expenditures by benthivorous croaker (*Micropogonias undulatus*) in the northern Gulf of Mexico. Additionally, bottom hypoxia's disruption of the normal DVM behavior of rainbow smelt, which causes individuals to occupy epilimnetic waters during the day (see Fig. 5), may increase the risk of being consumed by visual predators such as walleye (Brandt et al. 2011). A similar hypothesis was suggested during the hypoxia season in Chesapeake Bay (Costantini et al. 2008). Loss of dark bottom waters as a refuge from visual predators may further increase energy expenditures by causing individuals to be more vigilant of predators. In turn, the time available for rainbow smelt to forage on their own zooplankton prey might decrease (sensu Pangle et al. 2012).

Long-term effects of hypoxia on fish population dynamics

Rainbow smelt

Beyond direct mortality events that may occur (Rao et al. 2014), we predicted that the combined effects of physiological stress, reduced food availability, and increased predation (sensu Brandt et al. 2011) during hypoxic conditions would cause the central Lake Erie rainbow smelt population to decline. We did indeed find a significant negative relationship between the areal extent of hypoxia and central basin rainbow smelt abundance, even after accounting for possible confounding effects of walleye predation. Further, the combined negative influence of both hypoxia and walleye was stronger than either variable was individually. This latter finding suggests that the effects of top-down control of the planktivorous fishes in Lake Erie (Knight et al. 1984; Knight and Vondracek 1993) can be strengthened by hypoxia. Given the lack of study on piscivore–planktivore interactions in Lake Erie during the hypoxia season, we recommend future studies into how hypoxia affects foraging of predators.

Interestingly, suitable high-quality habitat for rainbow smelt exists in the bottom waters of Lake Erie's eastern basin during summer. However, it is unknown to what extent rainbow smelt can migrate into the cooler, well-oxygenated eastern basin to escape hypoxia. While rainbow smelt may move into the east basin in response to hypoxia, their movements may be blocked by the shallow Pennsylvania and Clear Creek ridges, which appear to be dominated by poor-quality habitat (i.e., GRP < 0 g·g^{-1}·day^{-1}). In support of this notion, we found that along the eastern portion of the central basin (transect D), the shallow Clear Creek and Pennsylvania ridges intersect the thermocline, which would force fish to swim through areas of negative GRP on their way to the eastern basin. Our acoustic survey of the area showed that fish aggregated at the base of this ridge in the area of highest habitat quality (see Fig. 4). Thus, years of large hypoxic extent may cause rainbow smelt to become trapped in the central basin, which may increase their risk of predation by walleye (Brandt et al. 2011). Even though rainbow smelt may become trapped in the central basin during the fall, the east basin population may still move into the central basin during better conditions during spring and early summer. Thus, while the central basin may become uninhabitable for rainbow smelt year-round with worsening hypoxia, eastern basin populations may still act as a source and provide prey resources to walleye in the central basin.

Similarly, aggregations at the edge of the hypoxic zone (aka "dead zone" may also increase susceptibility of rainbow smelt to commercial fishing. In support for the notion that commercial

fishers are successfully targeting hypoxia-induced aggregations of rainbow smelt, we found commercial catches of rainbow smelt in Canadian waters of Lake Erie to be higher during years with a larger area of hypoxia in the central basin relative to years with a smaller area, especially at the eastern boundary of the central basin. The following excerpt from an interview of a Lake Erie commercial fisher (who typically targets yellow perch, not rainbow smelt) on National Public Radio's *Living on Earth* (http://www. loe.org/shows/shows.html?programID=05-P13-00040; Saito 2005) also supports our contention:

> "SAITO [host]: Back at the dock, Joe Herr and his crew laugh when they hear people worrying about Lake Erie's dead zone. Lake Erie's fisheries are more productive than all the other Great Lakes combined and Herr has lasted nearly 50 years on Lake Erie because he has adapted to its changes. These days, he uses a depth finder to look for Lake Erie's dead zone, and plans accordingly.
>
> HERR [fisher]: We know where it should be so we go set our nets ahead of time and wait for it and herd the fish to us."

Given that bottom hypoxia has been shown to increase catchability in fishery-independent trawl assessment surveys in Lake Erie (e.g., yellow perch; Kraus et al. 2015a), as well as in commercial fisheries in other ecosystems (Langseth et al. 2014; Purcell et al. 2017), we strongly recommend further exploration into the linkages that exist among bottom hypoxia, fish behavior, fisher behavior, and fishing yields.

Emerald shiner

Similar to rainbow smelt, we found a negative correlation between hypoxia severity and emerald shiner abundance. The reasons for this relationship are more enigmatic, given that hypoxia's influence on emerald shiner habitat quality was less than that of rainbow smelt. While we can only speculate, this relationship could be due to reduced access to benthic prey during the hypoxia season (Arend et al. 2011) or intensified competitive interactions with rainbow smelt, owing to fish being forced higher up into the water column to avoid hypoxia (Pothoven et al. 2009).

Summary and conclusions

We have shown that the presence of bottom hypoxia in the central basin of Lake Erie can affect the short-term behavior and performance of central Lake Erie fish populations, but that the effect is species-dependent. Through the use of modeling, field collections, and laboratory analyses, we demonstrate that hypoxia disrupts the DVM behavior of rainbow smelt, which in turn causes short-term reductions in benthivory (in favor of planktivory), prey consumption, somatic growth, energetic condition, and benthic abundance. Similar acute alterations in movement and feeding behavior and negative consequences on performance (e.g., consumption, condition, growth) were not evident in emerald shiners, however. Model predictions showed that altered DVM behavior, and its subsequent effects on performance, were driven by reductions in habitat quality (as measured by GRP), which was severely restricted in the central basin of Lake Erie during peak hypoxia. By contrast, large areas of positive emerald shiner GRP remained during this time. These differences likely are due to different thermal preferences, with rainbow smelt being forced out of their preferred cold-water bottom habitat, whereas emerald shiners can remain in oxygenated surface waters within their preferred thermal range. Bottom hypoxia not only reduces the overall habitat suitability for rainbow smelt in central Lake Erie, it also forces fish to move horizontally (to hypoxia edges) or vertically (above the hypolimnion) to avoid areas of the lowest DO.

These shifts in habitat and short-term performance may come with a suite of long-term consequences, including increased susceptibility to predation and commercial fishing. While both emerald shiners and rainbow smelt catches were negatively related to hypoxia extent, we expect the negative impact of hypoxia to be worse for rainbow smelt, owing to its need for cold-water habitat that is only found in the hypolimnion during summer in central Lake Erie. With hypoxia predicted to increase as a result of continued climate change in Lake Erie (Collingsworth et al. 2017), owing to anticipated increases in temperature and nutrient runoff that are expected to strengthen and lengthen thermal stratification and perhaps bacterial respiration (Bosch et al. 2014; Scavia et al. 2014; Rucinski et al. 2016), rainbow smelt could be excluded from the central basin completely in future years. This notion would be especially likely if access to the eastern basin is cut off due to hypoxia as our data suggest is the case. Given the importance of rainbow smelt as a forage species in central and eastern Lake Erie, and its ability to support commercial fisheries, we encourage continued research into whether hypoxia indeed leads to increased walleye predation, commercial catchability, and reduced movement into the eastern basin. Additionally, because rainbow smelt are known predators on the early life stages of other economically important fishes (e.g., yellow perch), investigation into whether hypoxia-induced reductions in rainbow smelt are benefitting other species seems warranted. Owing to the similarity of Lake Erie to other ecosystems with respect to the response of its pelagic and benthopelagic food web to hypoxia (e.g., northern Gulf of Mexico: Hazen et al. 2009; Zhang et al. 2009; Chesapeake Bay: Costantini et al. 2008; Ludsin et al. 2009), a more complete understanding of hypoxia's long-term impacts on Lake Erie's planktivore community could better position management agencies in Lake Erie and coastal ecosystems alike to understand, predict, and manage the dynamics of their valued fisheries both now and in the face of continued climate change.

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Appendix A. Growth rate potential (GRP) modeling

The following is a description of GRP modeling conducted to assess habitat quality for rainbow smelt and emerald shiners in central Lake Erie during August (pre-hypoxia), September (hypoxia), and October (post-hypoxia), 2005.

Bioenergetics modeling

Growth rate potential (g·g⁻¹·day⁻¹) was modeled using the following general equation:

$$(1) \qquad G = [C - (R + SDA + F + U)]\frac{cal_z}{cal_f}$$

where C is consumption, R is respiration, SDA is specific dynamic action, F is egestion, and U is excretion, all of which is scaled by the difference in energy density between zooplankton prey (cal_z) and modeled fish (cal_f).

The structure and parameterization of the smelt model was based on Lantry and Stewart (1993). This model was developed specifically for Great Lakes applications. Lantry and Stewart (1993) used different parameter values for young-of-year (age 0), yearling (age 1), and adult (age 2+) rainbow smelt, which helps account for their increasing physiological sensitivity to and aversion of warm water temperatures as individuals age. We chose to use the yearling parameter values for our habitat quality modeling, as they represent an intermediate sensitivity to temperature and therefore could offer a conservative estimate of their sensitive for the mixed ages of individuals that we captured in central Lake Erie.

The only deviation from the Lantry and Stewart (1993) rainbow smelt growth model was the incorporation of a function (f_{DO}) developed by Arend et al. (2011) that accounted for the effect of hypoxia on smelt consumption rates. Following Arend et al. (2011), C is multiplied by the coefficient f_{DO}, calculated as

$$f_{DO} = min\left[\left(\frac{1}{0.16833T + 1.635}\right)DO, 1\right]$$

where T is water temperature (°C), and DO is dissolved oxygen concentration (mg·L⁻¹). This function accounts for the negative effect of DO on consumption (Chabot and Dutil 1999; Stierhoff et al. 2006; Brandt et al. 2009; Roberts et al. 2011). We assumed that C increases linearly with DO concentration from 0 to 1 up to a threshold DO concentration (DO_{crit}), above which f_{DO} equals 1 (Bartell 2003). Because increases in water temperature can magnify the effect of hypoxia on C (Schurmann and Steffensen 1997; Valverde et al. 2006; Marcek et al. 2020), we further assumed a negative relationship between DO_{crit} and water temperature.

The structure and parameterization of the emerald shiner growth model was identical to that of Arend et al. (2011), which, like the rainbow smelt model, was developed specifically for Great Lakes applications and includes the same f_{DO} function.

Table A1. Monthly wet weight (g) and energy density (J·g⁻¹) of rainbow smelt and emerald shiners used in growth rate potential models.

Species	Wet weight (g)			Energy density (J·g⁻¹)		
	August	September	October	August	September	October
Rainbow smelt	12.1	12.4	12.9	6742	6479	5754
Emerald shiner	2.3	2.7	3.5	6105	6971	7301

Inputs into the GRP included water temperature and DO observed by the plankton sampling system during daylight transects before (August), during (September), and after (October) hypoxia along transect B in 2005 and transect D in 2007. Other inputs included observed wet weight (g) and energy density (J·g⁻¹) of rainbow smelt and emerald shiners. We used the average values of these variables from the fish collected at the diel station located on transect B in 2005 for each month for which the model was applied (Table A1). Instead of incorporating a functional relationship in which observed zooplankton densities could serve as an input to consumption rates, we assumed that fish were always consuming at their maximum rates. This assumption likely leads to an overestimate of growth, particularly for rainbow smelt, for which we observed reductions in prey consumption during hypoxia. Subsequently, our predicted reductions in habitat quality experienced by rainbow smelt during hypoxia are likely conservative.

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